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Effects of Fragmentation on Species Retention in National Parks

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EFFECTS OF FRAGMENTATION ON SPECIES RETENTION IN NATIONAL PARKS

being

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of the Fort Hays State University
in Partial Fulfillment of the Requirements for
The Degree of Masters of Science

by

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PREFACE

This thesis is written in the style of the Journal of Biological Conservation.

Keywords: national parks, birds, mammals, island biogeography, conservation biology

ABSTRACT

The North American landscape is becoming increasingly fragmented, resulting in habitat patches with decreased area and increased isolation. Often, these patches exist as protected areas, such as national parks. The Theory of Island Biogeography is frequently used as a model for these patches, where each park serves as an 'island' surrounded by a 'sea' of human-altered habitats. As such, species richness and extinctions in a park might be explained by its area.

For this study, I used regression models to examine the relationship between richness and area, as well as extinctions and area, for mammals and birds in national parks. Mammal models were also constructed without rodents. Due to their relatively small size, rodents have a low detectability, and are often under surveyed. As a result, excluding them might improve my models. Additionally, because area is unlikely to be the only factor influencing species retention, I also included national park age, national park latitude, and national park longitude as predictor variables. I found some support for the relationship between area and species retention in national parks. Both bird models indicate that area had a positive relationship with species retention while area did not have a significant relationship with any of the mammal models.

Understanding the biogeographic features affecting species retention in national parks allows managers to develop more informed management plans. It is important to preserve the area of national parks to conserve biodiversity in and around the parks by limiting the future effects of fragmentation.

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INTRODUCTION

Habitat loss and fragmentation are increasing the number of global extinctions (Wilcox and Murphy 1985; Hanski 2005). Habitat loss and fragmentation can result from natural and human causes. Natural causes include glaciation, fires, and floods (Collinge 1996). Human causes include urbanization, agriculture, and climate change (Andrén 1994). These events, and the resulting landscape fragmentation, result in an overall loss of habitat, which leads to the dismantling of communities and subsequent formation of new communities (Quintero and Wiens 2013). Species that are not able to adapt or move, go extinct (Nogués-Bravo et al. 2018). Currently, habitat loss and fragmentation are occurring at high rates due to human activities (Collinge 1996). Populations and communities are increasingly disrupted, resulting in more extinctions than would occur naturally (Barnosky et al. 2011). Wilcove et al. (1986) stated that fragmentation is "… the principal threat to most species in the temperate zone." In North America, the landscape is being converted by agriculture and urbanization, leading to the loss of large areas of continuous habitat (Collinge 1996). This conversion results in natural habitat patches with decreased area, increased isolation, and increased edge (Wiens 1995; Collinge 1996).

Fragmentation has several effects on the organisms present on the landscape. The overall loss of habitat, as well as decreased patch size, leads to reduced resources. Without enough resources to sustain prior population levels; populations inevitably decrease (Pickett and Thompson 1978). Fragmentation also increases isolation between habitat patches (Zuidema et al. 1996; Berg 1997). In turn, increased isolation affects resources gathering. Because organisms must travel across inhospitable habitat to gather resources, their ability to gather resources is reduced. The increased isolation of habitat patches also decreases movement amoung metapopulations. Without this connectedness, the probabililty of a subpopulation being recolonized after extinction is reduced (Wiens 1995). Species composition also might be altered. Increased edge resulting from fragmentation can lead to increased richness and abundance of generalists that prefer edge habitat and decreased richness and abundance of specialist species that require resources found in interior habitats (Collinge 1996). Additionally, predation rates are typically higher at the edge. Sensitive specialists suffer from decreased interior habitat and increased edge habitat, exposing them to higher predation rates (Wiens 1995).

Some species will be more sensitive to fragmentation than others (Diamond 1975; Patterson 1984; Collinge 1996). Species that have small geographic ranges, low densities, and are higher on the food chain are more vulnerable to extinction (Purvis et al. 2000). Populations of R-selected species are more likely to be maintained after fragmentation than are populations of K-selected species (Keinath et al. 2017). However, due to the small size of many R-selected species, they might be less likely to be detected in surveys. Additionally, due to their increased sensitively to random events, small populations have a higher risk of extinction as a result of fragmentation (Pickett and Thompson 1978). The biological effects of fragmentation also depend on the quality of the remaining habitat patches and the effect of human activity in the surrounding landscape (Collinge 1996; Piekielek and Hansen 2012).

Nature reserves, like national parks, are protected natural areas that typically exist as patches (Newmark 1986a). Often, they are relatively small and isolated, making them vulnerable to land use change (Rivard et al. 2000). As the landscape becomes increasingly fragmented, nature reserves experience decreased connectedness. Additionally, the patches of native habitat in which the reserves are embedded in decrease in area (Diamond 1975).

Authors have suggested that the fragmentation of the landscape results in natural habitat patches analogous to islands (Diamond 1975; Pickett and Thompson 1978; Newmark 1986a; Collinge 1996; Rivard, et al. 2000). The Theory of Island Biogeography, described by MacArthur and Wilson in 1967, is frequently used as a model for these patches. Each patch of natural habitat serves as an 'island' surrounded by a 'sea' of human-altered habitat. The Theory of Island Biogeography is based on two key ideas. The first is that species richness is related to area and driven by extinctions; an idea known as the species-area relationship. The other idea is that species richness, through immigration constraints, is related to isolation. If nature reserves are analogous to islands, then species richness in any given nature reserve can be explained by the reserve's area and isolation. However, isolation in these reserves is extremely hard to measure. Unlike true islands, the area around reserves is not completely inhospitable (Wiens 1995). The fragmented landscape is not as effective as water in limiting dispersal. Measuring isolation would, therefore, be extremely difficult. This paper will instead focus on the relationship between area and species retention in national parks. National parks are a prime study system for this theory because they are well studied, vary in age and area, and are distributed across the contiguous U.S.

Species retention is the amount of species that currently remain in an area relative to the amount of species that historically existed there. Species retention can be examined through current species richness patterns. A relationship between the current species richness and the area of parks suggests that the retention of species in parks might be differing between different park sizes. Parks with higher species richness are likely retaining more species. Species retention can also be examined with extinctions. Since extinctions takes into account historical richness, it is a more direct measurement of retention. Parks with fewer extinctions are likely retaining more species.

Mammals and birds are well-documented groups. Previous research has documented that both groups follow the species-area relationship (Newmark 1986b; Rahbek 1997). For these reasons, mammals and birds were used in this study to examine richness and extinction patterns in national parks. These two taxonomic groups also have several differences which might result in different responses to fragmentation. Due to the migratory nature of many birds, they are more likely to experience threats outside the national parks than are mammals, whose threats will largely be contained within the park (Rivard et al. 2000). Additionally, mammals tend to have higher population densities and lower vagility than birds (Silva et al. 1997). Vagility impacts an organism's ability to disperse and gather resources, particularly in a fragmented system. Bird distributions also tend to be better documented than mammals, because of recreational bird watching.

Factors other than area and isolation might also influence species richness and extinctions in national parks (Boecklen and Gotelli 1984). The decrease in species richness in higher latitudes, otherwise known as the latitudinal gradient in species richness, can also impact how many species are present in each park (Gaston 2000). Additionally, as a general pattern, European settlers began settlement in the Eastern United States and expanded westward, resulting in a temporal gradient in fragmentation from east to west. Therefore, longitude can be used as a proxy variable to examine the influence of time since fragmentation on species richness and extinctions. Finally, age of the park can also impact species retention. Habitat around both young and old parks have been experiencing fragmentation for roughly the same amount of time. Areas within park boundaries experience less habitat degradation than areas outside. Therefore, habitat in older parks is likely to be less degraded, which might improve species retention. Including these additional variables gives us a more holistic understanding of the factors influencing species richness and extinctions.

In this study, I seek to determine whether area affects the retention of species in national parks. This will be examined through patterns of current species richness and extintions in mammals and birds. Park age, latitude, and longitude are included in the models to account for other sources of potential variation.

METHODS AND MATERIALS

I examined patterns of extinctions and richness of birds and mammals in 40 national parks (Fig. 1) relative to park area, park age, and park location (latitude and longitude). These patterns were explored with regression models. Spatial analyses were performed in ArcGIS version 10.5.1 (ESRI 2018). Statistical analyses were performed in R x64 version 3.3.1 (R Core Team 2018).

Variables

In this study, the primary predictor variable is national park area. I obtained the area of each national park via the National Park Service website (NPS, www.nps.gov/aboutus/national-park-system.htm, accessed September 22, 2018). Only NPS properties that were designated as national parks were used in the models, while other areas such as national monuments were excluded. National parks tend to be better studied due to their popularity. I excluded national parks that were outside the contiguous U.S. or parks that were true islands. Island parks were excluded because of the additional factors that influence their connectedness with other terrestrial habitat (particularly water). Two additional parks were also excluded from these analyses: Hot Springs National Park and Pinnacles National Park. Hot Springs National Park is a settlement built around hot springs. It does not represent a natural landscape and is therefore not relevant to this study. I excluded Pinnacles National Park because it was created in 2011. I only included parks that were at least 10 years old because younger parks likely have not existed long enough to influence the richness of the animals present. In the National Park Service's database, the current species lists for Sequoia National Park and Kings Canyon National Park are combined. Therefore, for my analyses, I considered the two parks as one unit.

I included additional predictor variables to improve the models and explain as much variation in species richness as possible. These variables include national park age as of 2017, national park latitude, and national park longitude (Appendix A). National park latitude and longitude were calculated from the centroid of the polygon shapefile for each park. I downloaded the National Park Service – Park Unit Boundaries shapefile from the National Park Service website (https://public-nps.opendata.arcgis.com/datasets/national-park-service-park-unit-boundaries, accessed September 22, 2018).

I constructed two sets of models: one model with richness as the response variable and another model with percent extinction as the response variable. I used two separate taxonomic groups to perform the analyses: birds and mammals. Models for the different taxonomic groups were performed separately because each taxonomic group is surveyed differently and therefore have different levels of accuracy. Species in the order Rodentia are generally small bodied, secretive, nocturnal, and semi-cryptic with their environment. As a result, they are often under-surveyed, which can result in biased measures of species richness. To examine this potential bias, I developed mammal models with and without rodents.

I obtained park species lists for each taxonomic group to calculate richness. Richness data were obtained through the Integrated Resource Management Applications (IRMA) for the National Park Service (https://irma.nps.gov/NPSpecies/, accessed September 22, 2018). I defined richness as the number of native mammal or bird species within each park. I edited the mammal and bird species lists for each park to remove non-native or unconfirmed species. Most non-natives in parks result from human introduction. This thesis aims to describe the natural system reacting to the fragmentation of the landscape. It must be noted, however, that introduced species might affect the native species that are present. I removed unconfirmed species to increase confidence in the models. I also updated and standardized the nomenclature for the species in the park lists.

I defined extinctions as instances where an organism was historically present in a park (according to its historic range) but is not on the park's current species list. I downloaded historic range maps for each mammal species from NatureServe http://www.natureserve.org/conservation-tools/digital-distribution-maps-mammals-western-hemisphere, accessed October 1, 2018) and for each bird species from Bird Life International (http://datazone.birdlife.org/species/requestdis, accessed October 1, 2018). These shapefiles included both introduced and native ranges. For each species, I removed introduced ranges before calculating historic richness. If a species historic geographic range included a park, I assumed that the species was historically present at that park. By counting how many species' historic ranges included each park, I was able to estimate the historic richness of the parks. A species that is currently present in a park, but undetected, will be counted as an extinction if its historic range included the park. To decrease the number of these 'false extinctions', I only included species that are currently document in national parks in my analyses. However, this approach might underestimate the number of extinctions in each park. Because the number of extinctions is likely influenced by historical species richness, I used the extinction percentage as a standardized measure to account for differences in historical richness among the parks. To calculate percent extinctions, I divided the number of extinctions by the historic richness for each park.

Analysis

Before developing the models, the predictor variables were tested for multicollinearity with variation inflation factors (VIF). In instances when I detected multicollinearity (VIF>5), I removed one of the correlated predictor variables. I developed each model with the remaining predictor variables. Then, I checked the models for heteroscedasticity, normality of residuals, and outliers with Q-Q plots. I applied transformations where necessary to ensure the data met the assumptions of the procedure.

Models were developed in R and initially included all predictor variables. For each response variable, I conducted a backward step-wise regression to select the best model based on the lowest Akaike Information Criterion (AIC). I removed non-significant predictor variables and repeated the models. Area was always included, regardless of significance, because area was the main predictor variable of interest in this study.

RESULTS

This study included 40 national parks in the contiguous United States (Fig. 1). These parks ranged in size from 107.4 km^2 to 13,650.3 km^2 (Appendix A). The youngest park included in this study was Great Sand Dunes National Park at 14-years-old, and the oldest park was Yellowstone National Park at 146-years-old.

Big Bend National Park had the greatest bird richness at 402 species and Mount Rainier National Park had the lowest with 152 species (Appendix B). The park with the greatest mammal richness was Grand Canyon National Park with 87 species, while Biscayne National Park had the lowest mammalian richness with 16 species (Appendix C). When I removed rodents, Big Bend National Park, Grand Canyon National Park, and Yosemite National Park had the most mammals with 48 species each, and Biscayne National Park had the fewest with 11 species of mammals (Appendix D). No multicollinearity was detected amoung the predictor variables (Table 1).

Birds

The best-supported model for bird richness in national parks included the log transform of area and latitude as predictor variables (Table 2). This model can be used to explain 42.4% of the variation in bird richness across the 40 national parks ($R^2=0.424$, F=15.3, df=2,37, p-value<0.001). The log transform of national park area had a significant positive relationship with bird richness (Fig. 2) and national park latitude had a significant negative relationship with bird richness (Fig. 3).

The best-supported model for percent bird extinctions in national parks included a Box-Cox transformation of area ($\lambda=0.6$) as the sole predictor variable (Table 2). This model explained 20.5% of the variation in the percentage of bird extinctions ($R^2=0.205$, F=11.1, df=1,38, p-value=0.0019). Area had a significant negative relationship with percent extinctions (Fig. 4).

Mammals

The best-supported model for mammal richness in national parks included the Box-Cox transformation of national park area (λ=0.6), age, and longitude as predictor variables (Table 3). This model explained 44.1% of the variation in the richness of mammals in national parks (R^2=0.441, F=11.3, df=3,36, p<0.001). Area had a non-significant relationship with mammal richness (Fig. 5), age had a significant positive relationship with mammal richness in (Fig. 6), and longitude had a significant negative relationship with mammal richness (Fig. 7).

The best-supported model for percent mammal extinctions in national parks included area, age, and the log transform of latitude as predictor variables (Table 3). This model explained 17.2% of mammal percent extinction in national parks (R^2=0.172, F=3.70, df=3,36, p-value=0.020). Percent mammal extinctions had a non-significant relationship with national park area (Fig. 8), a significant negative relationship with national park age (Fig. 9), and a significant negative relationship with national park latitude (Fig. 10).

Mammals without rodents

The best-supported model for mammal richness without rodents included national park age, national park area, and national park longitude as predictor variables (Table 4). This model explained 40.8% of mammal richness without rodents (R^2=0.408, F=9.97, df=3,36, p-value<0.001). Mammal richness without rodents had a non-significant relationship with national park area (Fig. 11), a significant positive relationship with national park age (Fig. 12), and a significant negative relationship with national park longitude (Fig. 13).

The best-supported model for percent extinctions of mammals without rodents included national park area and the log transform of national park latitude as predictor variables (Table 4). This model explained 19.9% of the variation in the percentage of mammal extinctions without rodents (R^2=0.199, F=4.22, df=3,36, p-value=0.012). Mammal percent extinctions without rodents had a non-significant relationship with national park area (Fig. 14), a significant negative relationship with latitude (Fig. 15), and a marginally significant negative relationship with national park age (Fig. 16)

DISCUSSION

Studies suggest nature reserves, like national parks, behave as land-bridge islands (Diamond 1975; Pickett and Thompson 1978; Newmark 1986a; Collinge 1996; Rivard, et al. 2000). As such, species richness in any given park is a function the area and isolation. According to the Theory of Island Biogeography, extinctions in national parks can be largely explained by area. Additionally, other factors such as park age, latitude, and longitude can affect extinctions and richness in these reserves (Table 5). This study documented some support for this theory when the additional factors are included.

Birds

The best-supported model for bird richness in national parks included the log transform of area and latitude as predictor variables. The model indicated a positive relationship between the log transform of area and bird richness (Fig. 2). This means that as park size increases, bird richness also increases. This trend is expected, given the species-area relationship. In this relationship, richness increases with area (MacArthur and Wilson 1967). The model also indicated a significant negative relationship between bird richness and national park latitude (Fig. 3). This indicates that northern parks tend to have fewer bird species than southern parks. This result is expected, given the latitudinal gradient in species richness. In this pattern, species richness decreases as latitude increases (Gaston 2000).

The best-supported model for the percentage of bird extinctions in national parks included the Box-Cox transformation of area as the sole predictor variable. Bird percent extinctions had a significant negative relationship with area (Fig. 4). Therefore, the percentage of extinctions decreases with an increase in national park area. Larger parks should theoretically hold larger populations. Larger populations have a decreased probability of extinction (MacArthur and Wilson 1967), which might explain this pattern.

Mammals

The best-supported model for mammal richness in national parks included the Box-Cox transformation of area, age, and latitude as predictor variables. Mammal richness had a non-significant relationship with the Box-Cox transformation of national park area (Fig. 5). Normally, non-significant results would be eliminated in a step-wise regression. However, area is the main predictor variable of this study and was included in all models. Mammal richness might not show a relationship with area because the area of national parks is arbitrary. National parks are embedded in larger habitat patches, so mammals may be responding to the larger habitat patch, rather than the park boundaries.

Age of national parks had a significant positive relationship with mammal richness (Fig. 6) and suggests that older parks have higher richness than younger parks. Because older parks have been established longer, they have experienced less habitat degradation prior to their formation than have younger parks. As a result, species retention might be greater in older parks. Mammal richness also had a highly significant negative relationship with national park longitude (Fig. 7). This indicates that western parks have greater species richness than eastern parks. This might be because western parks tend to be older and larger than eastern parks, and both variables in this study had positive relationships with species richness. Additionally, Europeans settled the east before the west, and therefore, eastern parks have been experiencing fragmentation longer than western parks.

The percentage of mammal extinctions in national parks was best explained using area, age, and the log transform of latitude as predictor variables. Area had a non-significant relationship with the percentage of mammal extinctions (Fig. 8). This might be due to unfulfilled extinction debt. Extinction debt is the idea that typically species do not go extinct immediately following an extinction-inducing phenomenon. Instead, there is a time period between the phenomenon and the extinction (Tillman et al. 1994). Therefore, area might still influence species extinctions but the effects are not yet detected.

National park age had a negative relationship with the percentage of mammal extinctions (Fig. 9). This pattern was marginally significant (p-value= 0.0755) and indicates that the percentage of extinctions might be lower in older parks than in younger parks. As with the pattern between mammal richness and national park age, this pattern might be the result of decreased habitat degradation within older parks. Because older parks like have experienced less habitat degradation, they might have higher species retention than younger parks. In this model, the log transform of latitude also had a negative relationship with the percentage of mammal extinctions (Fig. 10). This indicates that northern parks have a lower percentage of extinctions than southern parks. Northern states tend to be less populated (U.S. Census Bureau 2017), and this might result in less fragmentation. Northern parks are therefore embedded in more continuous habitat than southern parks, which might result in a decreased loss of species because of the increased abundance of surrounding habitat.

Mammals without rodents

The best-supported model for mammal richness without rodents included national park area, age, and longitude as predictor variables. This model explained 40.8% of the variation in mammal richness. This is lower than the 44.1% of variation explained in mammal richness when rodents were included (using age, latitude, and area as predictor variables).

I did not detect a relationship between mammal richness without rodents and national park area (Fig. 11). This matches what was found when rodents were included (Fig. 5).National park age had a positive relationship with mammal richness (Fig. 12). This indicates that mammal richness increases with age. I observed the same result when rodents were included (Fig. 6). Lastly, I detected a negative relationship between mammal richness without rodents and national park longitude (Fig. 13). This indicates that western parks have a higher mammal richness than eastern parks. The same pattern was observed in mammal richness when rodents were included (Fig. 7).

When I removed rodents, the best model for mammal percent extinctions included national park area, age, and the log transform of latitude as the predictor variables. This model accounts for 19.9% of the variation in the percentage of mammal extinctions. This is an increase from the 17.2% of variation explained in the mammal percent extinction model that included rodents.

The percentage of mammal extinctions did not have a significant relationship with national park area when rodents are excluded (Fig. 14). This is the same result as when rodents were included in the model (Fig. 8). The percentage of bird extinctions did had a significant negative relationship with area (Fig. 4), indicating that birds are going extinct due to decreased area. Mammals might not show this pattern due to extinction debt. Birds are more vagile and than mammals and are better able to move after an extinction inducing event. Mammals are more likely to stay in place and go extinct, rather than move on. Birds can also assess the landscape better while flying than mammals can from the ground. Therefore, birds are better able to select larger, more suitable habitat patches than mammals. As a result, birds can move from an area, causing a local extinction, while mammals are more likely to say in place and die over time.

When I excluded rodents from the analysis, the percentage of mammal extinctions had a marginally significant negative relationship with national park age (Fig. 16). When I included rodents, I observed the same marginally significant pattern (Fig. 9). The percentage of mammal extinctions had a negative relationship with the log transform of national park latitude (Fig. 15). This indicates that the percentage of mammal extinctions is lower in northern parks than in southern parks. I observed the same pattern when rodents were included (Fig. 10).

Conclusions

The results of this study had some support for the hypothesis that area affects the retention of species. The bird richness and bird percent extinction models both supported the hypothesis. Area had a significant positive relationship with bird richness and a significant negative relationship with bird percent extinctions. These models suggest that parks with larger areas have higher retention of species. Newmark (1986a) also observed this result in his models which utilized a small subset of mammals. However, all four of the mammal models in this study did not indicate a relationship between area and the retention of species. This might be due to unfulfilled extinction debt.

To improve the explanatory power of the models, other factors were included that might affect species retention. All four of the mammal models included age as a significant predictor variable. These models indicated that older parks had retained more mammal species than younger parks. Younger parks might have experienced more habitat degradation before being established while older parks have been protected longer and therefore might have experienced less habitat degradation. Better habitat quality likely results in greater species retention.

Latitude was included in the bird richness model and both of the mammal percent extinction models. The bird richness model indicates that northern parks have lower species richness compared to southern parks. This is consistent with the latitudinal gradient in species richness (Hillebrand 2004). Mammal richness did not have a significant relationship with latitude. However, mammal percent extinction models indicate that northern parks had higher species retention compared to southern parks. National parks are embedded in a landscape that differs in habitat quality. Northern parks tend to be embedded in more continuous habitat because of lower surrounding human density and activity. Northern parks may experience a decreased loss of species because of the increased abundance of surrounding habitat. Bird percent extinctions, however, did not have a significant relationship with latitude. Because of their migratory nature, birds require more area than mammals. As a result, retention of mammal species might be a function of small scale patterns like surrounding habitat, while retention of bird species might be a function of large scale patterns such as the latitudinal gradient in species richness.

Both mammal richness models included longitude as a predictor variable. These models indicate that western parks tend to have a higher species richness than eastern parks. This might be because western parks tend to be older and larger than eastern parks, both variables in this study were found to be predictors of higher species richness. Additionally, Europeans generally settled North America from east to west. As a result, the eastern landscape has been experiencing fragmentation longer than the western landscape which might allow western parks to retain more species than eastern parks.

To improve mammal models, richness and percent extinction models were developed with and without rodents. Removing rodents decreased the variation explained in the mammal richness model. The R^2 value for the mammal richness model decreased from 0.441 to 0.408 when rodents were removed. On the other hand, removing rodents increased the percent of variation explained in the percent extinction model. Removing rodents brought my R^2 from 0.172 to 0.199. These changes in R^2 values indicate that removing rodents increased the amount of variability that could be explained by the percent extinctions model, but reduced the amount of variability that could be explained by the richness model.

Overall, the models in this study had low R^2 values. The R^2 values ranged from 0.172 (mammal percent extinction model) to 0.441 (mammal richness model). Therefore, only 17.2-44.1% of the variation in the response variables was explained in these models. This indicts that factors other than area, latitude, longitude, and age influence species retention in national parks. One such factor is isolation. According to the Theory of Island Biogeography, richness on any given island is a function of the island's area and isolation. True islands are surrounded by water, which greatly reduces immigration potential. Conversely, national parks are embedded in a landscape of varying habitat quality. Therefore, potential for immigration will vary depending on the matrix and the dispersal ability of individual species. Placing a metric on immigration for species with differences in vagility across the landscape would be difficult. As a result, isolation was not included in this study. This is likely a large source of the unexplained variation. Other sources might include human impact (urbanization, roads, etc.), climate, and habitat heterogeneity. Each of these factors have been shown to affect species richness and retention (Berg 1997; Rivard et al. 2000; Pielieklek and Hansen 2012). Future studies should explore these variables as potential predictor variables.

Area of the national parks might also be a significant source of error. The boundaries of national parks are arbitrary and might not represent the true extent of the habitat patch in which the park is embedded. Therefore, the area of the park boundary is likely an underestimate of the true 'island' area. This might have influenced the models and might explain why area was not a significant predictor in the mammal models. Future studies might re-map the boundaries using habitat data to more accurately represent the size of the habitat patch in which each park is embedded.

My results suggest national parks are behaving as islands. As the continent becomes increasingly fragmented, the area of the habitat patches where the parks are embedded will decrease, and isolation will increase. This will likely result in further faunal collapse within national parks. Not only do national parks serve as nature reserves, they also benefit the surrounding land. National parks provide ecosystem services such as air purification through vegetation, water regulation, habitat for species, and ecotourism, along with many other services (Palomo et al. 2013). It is important to preserve the area of national parks to limit the future effects of fragmentation and conserve biodiversity in and around the parks. Additionally, understanding the biogeographic processes affecting species retention in national parks allows managers to develop more informed management plans. Maintaining habitat around the parks, as well as inside the borders, might help limit the amount of isolation from other areas of suitable habitat and allow for more overall habitat, both of which might help retain more species.

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Table 1. Multicollinearity test using variance inflation factor (VIF) between predictor variables (N=40). Values greater than five indicates high multicollinearity.

Explanatory variables	VIF
National park age	1.11
National park area	1.06
National park longitude	1.26
National park latitude	1.24

Table 2. Results of bird linear regression models for richness and percent extinctions in 40 national parks within the contiguous United States.

	Richness		Percent extinctions	
Variable	β	Transformation	β	Transformation
Area	26.5***	Log	-0.0710**	BoxCox
Latitude	-4.36**	--	--	--
Intercept	223**		0.518***	
R^2		0.424***		0.205**
F		15.3		11.1

*marginally significant ** p<0.05 ***p<0.001

Table 3. Results of mammal linear regression models for richness and percent extinctions in 40 national parks within the contiguous United States.

	Richness		Percent extinctions	
Variable	β	Transformation	β	Transformation
Age	0.124**	--	-8.32E-04*	--
Area	0.119	BoxCox	-1.19E-07	--
Longitude	-0.550***	--	--	--
Latitude	--	--	-0.234**	Log
Intercept	-9.09		1.13***	
R^2		0.441***		0.172**
F		11.3		3.70

*marginally significant ** p<0.05 ***p<0.001

Table 4. Results of mammal (no rodents) linear regression models for richness and percent extinctions in 40 national parks within the contiguous United States.

	Richness		Percent extinctions	
Variable	β	Transformation	β	Transformation
Age	0.094***	--	-9.71E-04*	--
Area	-2.66E-04	--	4.40E-06	--
Longitude	-0.242***	--	--	--
Latitude	--	--	-0.280**	Log
Intercept	4.46		1.31**	
R^2		0.408***		0.199**
F		9.97		4.22

*marginally significant **p<0.05 ***p<0.001

Table 5. Results for all models. Sign indicates the direction of the relationship. Zeros indicate no relationship and a blank cell indicates that the predictor variable was not used in the model.

Model	Taxonomic group	Predictor Variable Area	Age	Latitude	Longitude	R^2
Richness	Bird	+		-		0.424
	Mammal	0	+		-	0.411
	Mammal without rodents	0	+		-	0.408
Percent Extinctions	Bird	-				0.205
	Mammal	0	-	-		0.172
	Mammal without rodents	0	-	-		0.199

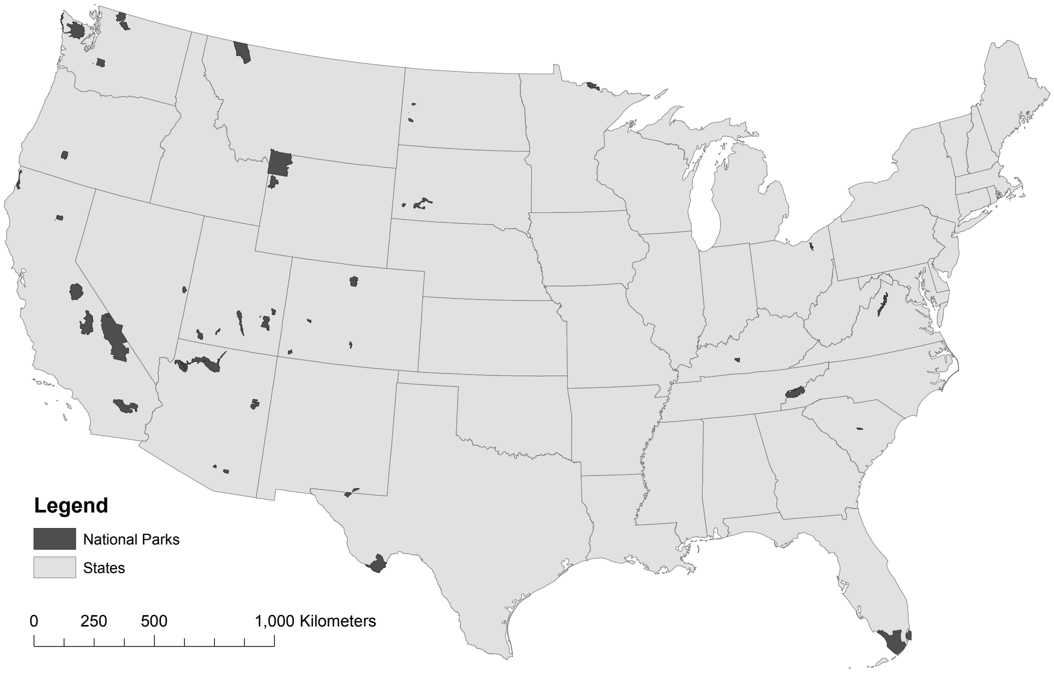

Figure 1. Map of the contiguous United States. National parks used in this study are indicated in dark gray (N=40).

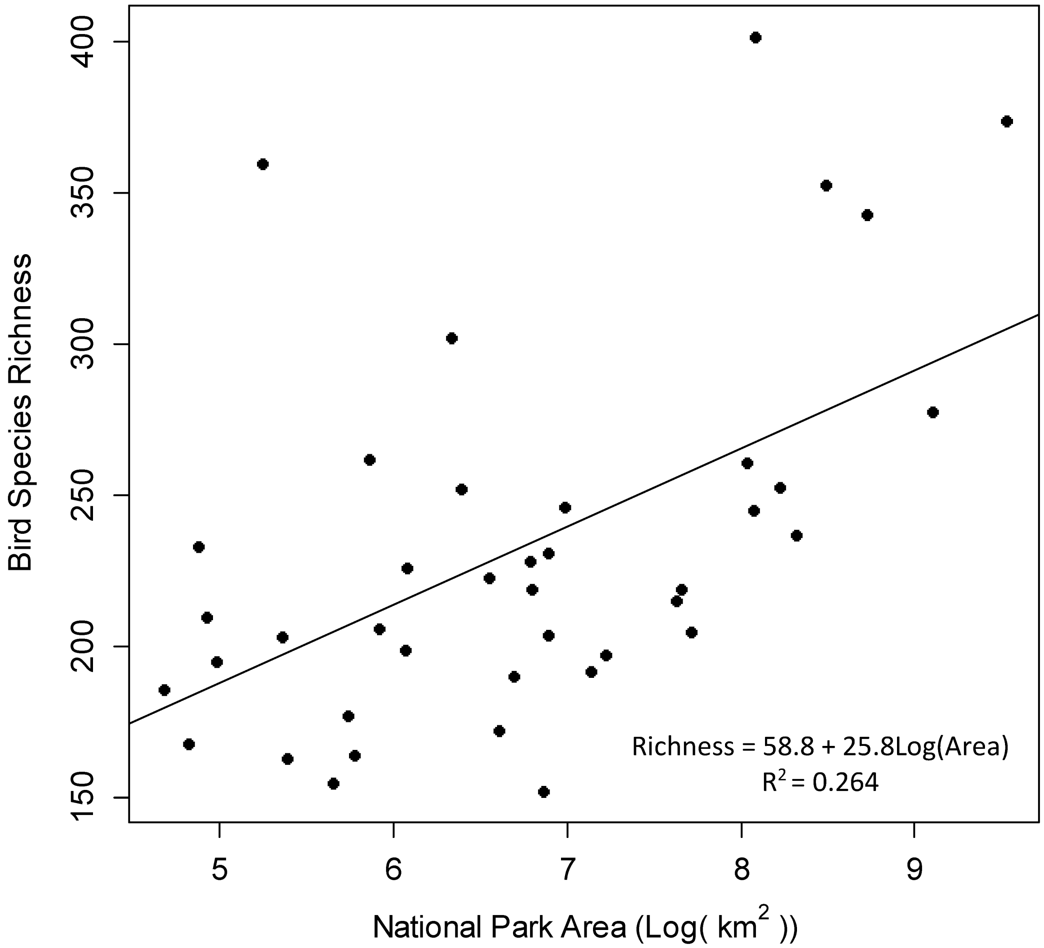

Figure 2. The relationship between bird species richness and the log transform of area (km^2) in 40 national parks of the contiguous United States (R^2=0.264, F=15.0, df=1,38, $p<0.001$).

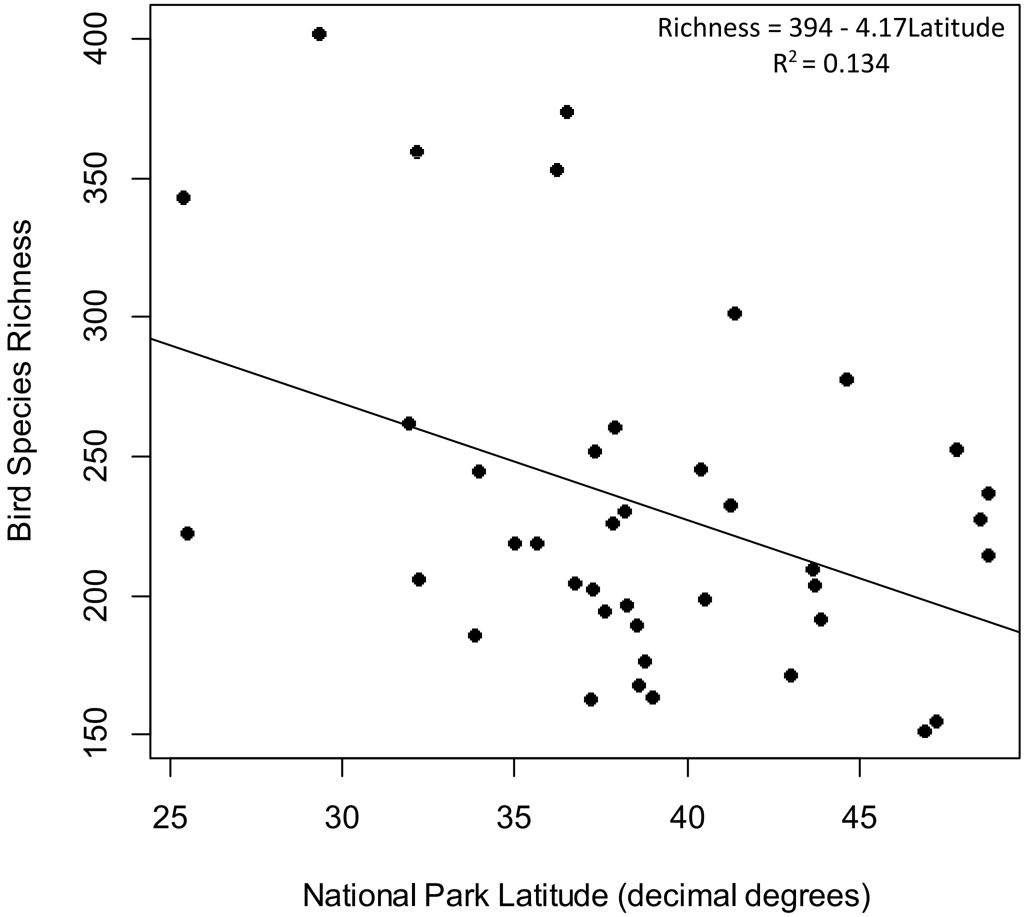

Figure 3. The relationship between bird species richness and latitude (decimal degrees) in 40 national parks of the contiguous United States (R^2=0.134, F=7.03, df=1,38, p=0.012).

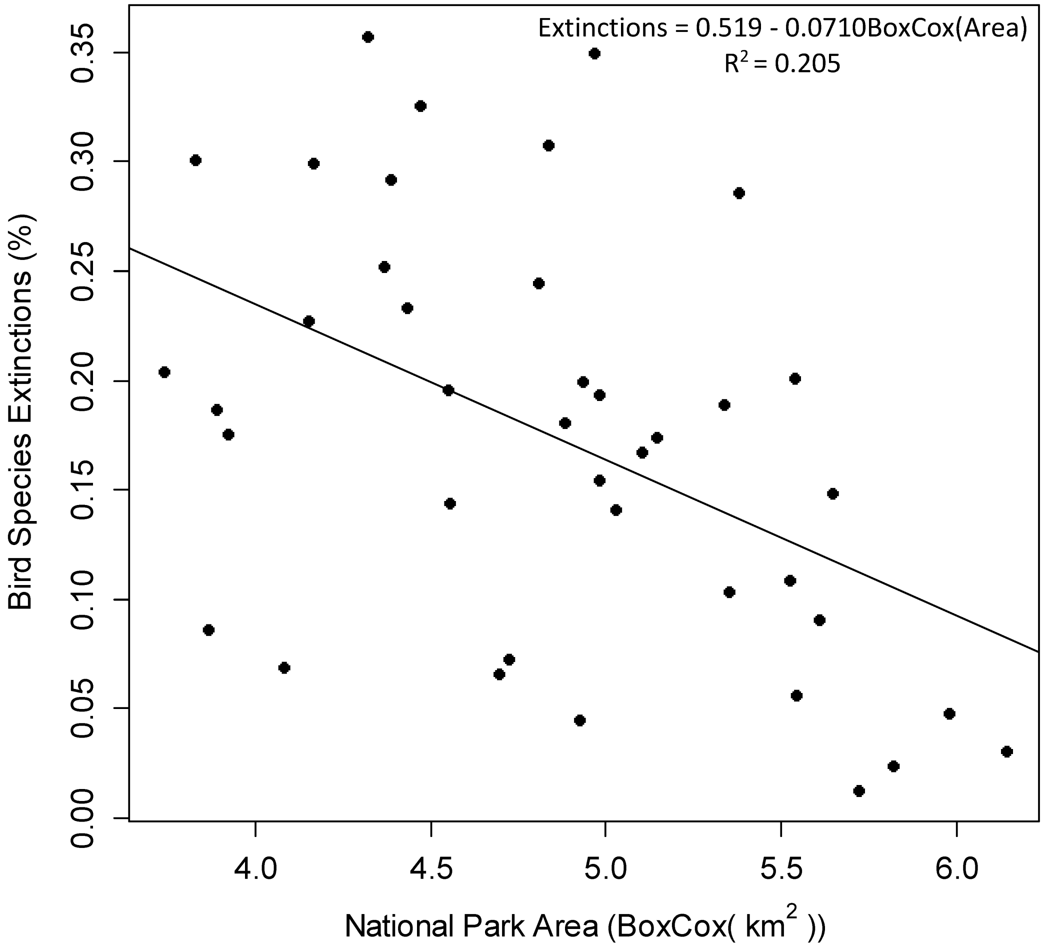

Figure 4. The relationship between the bird species extinctions (percent) and the Box-Cox transform of area (km^2, λ=-0.1) in 40 national parks of the contiguous United States (R^2=0.205, F=11.1, df=1,38, p=0.002).

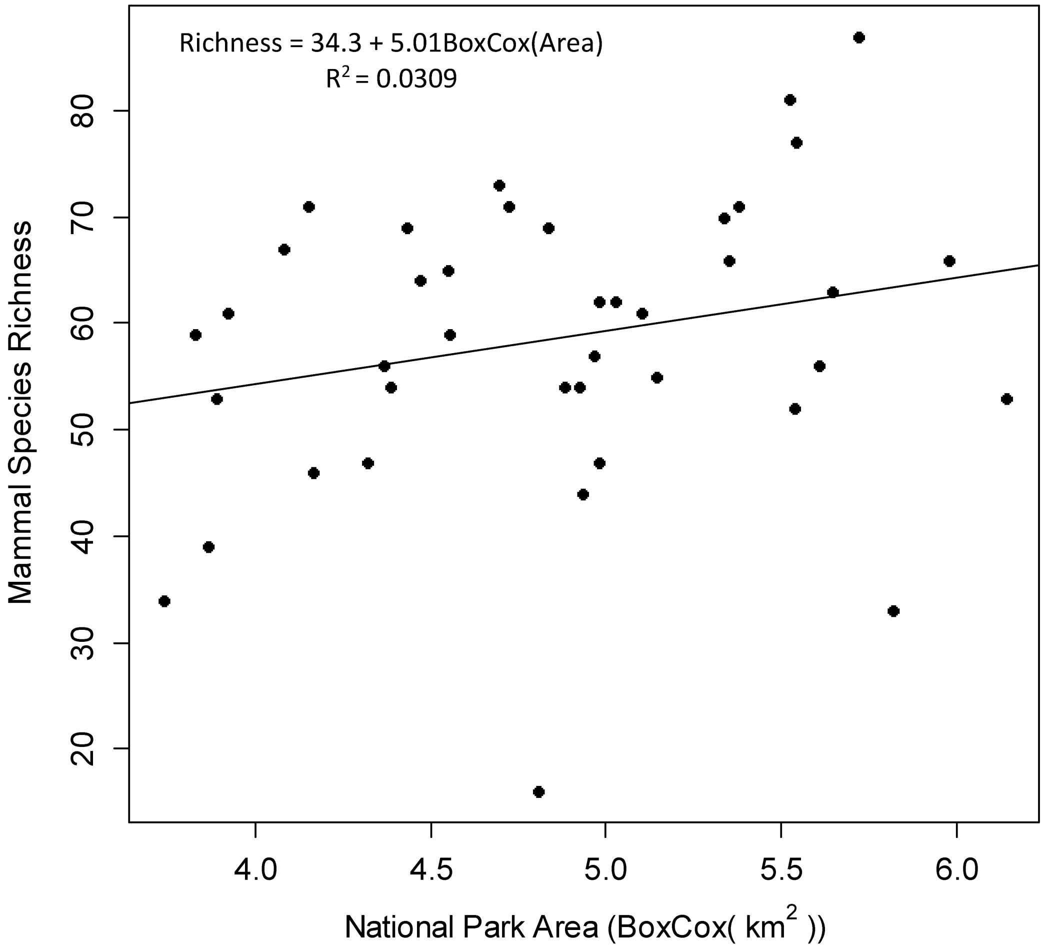

Figure 5. The relationship between mammal species richness and the Box-Cox transform of area (km^2, λ=-0.1) in 40 national parks of the contiguous United States (R^2=0.0309, F=2.241, df=1,38, p=0.143).

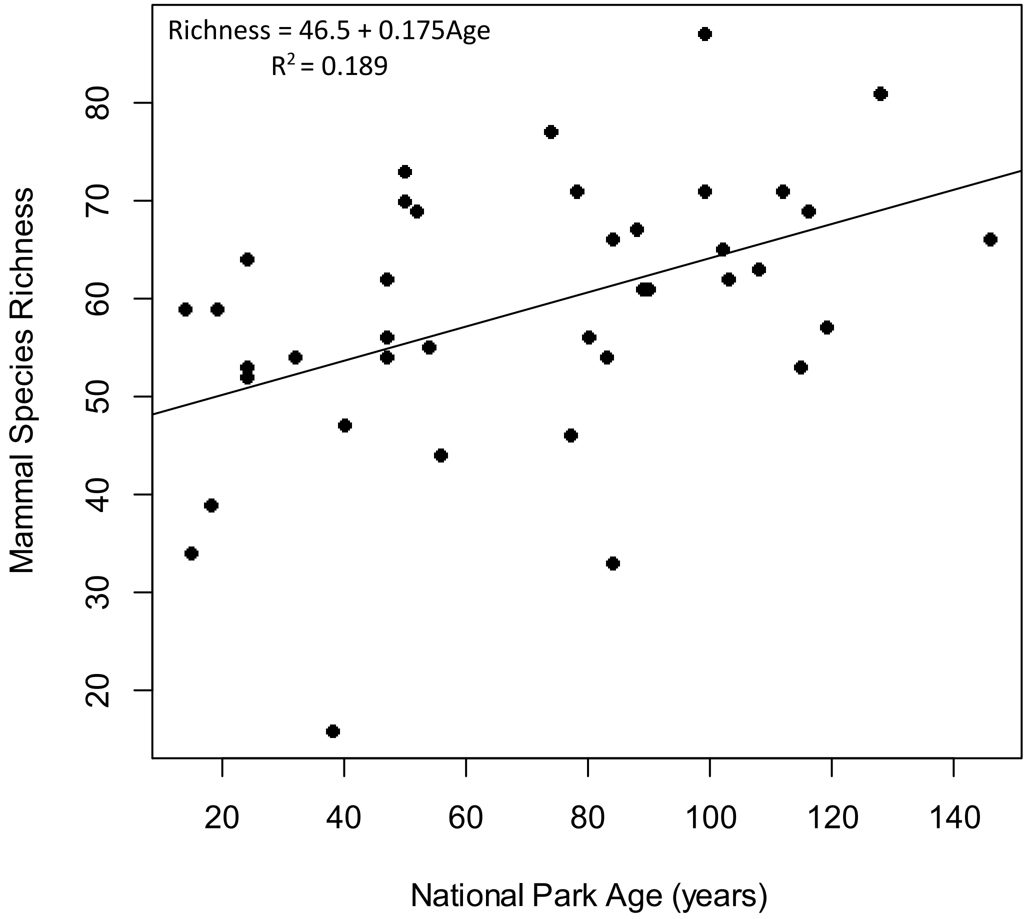

Figure 6. The relationship between mammal species richness and age (years) in 40 national parks of the contiguous United States (R^2=0.189, F=10.1, df=1,38, p=0.003).

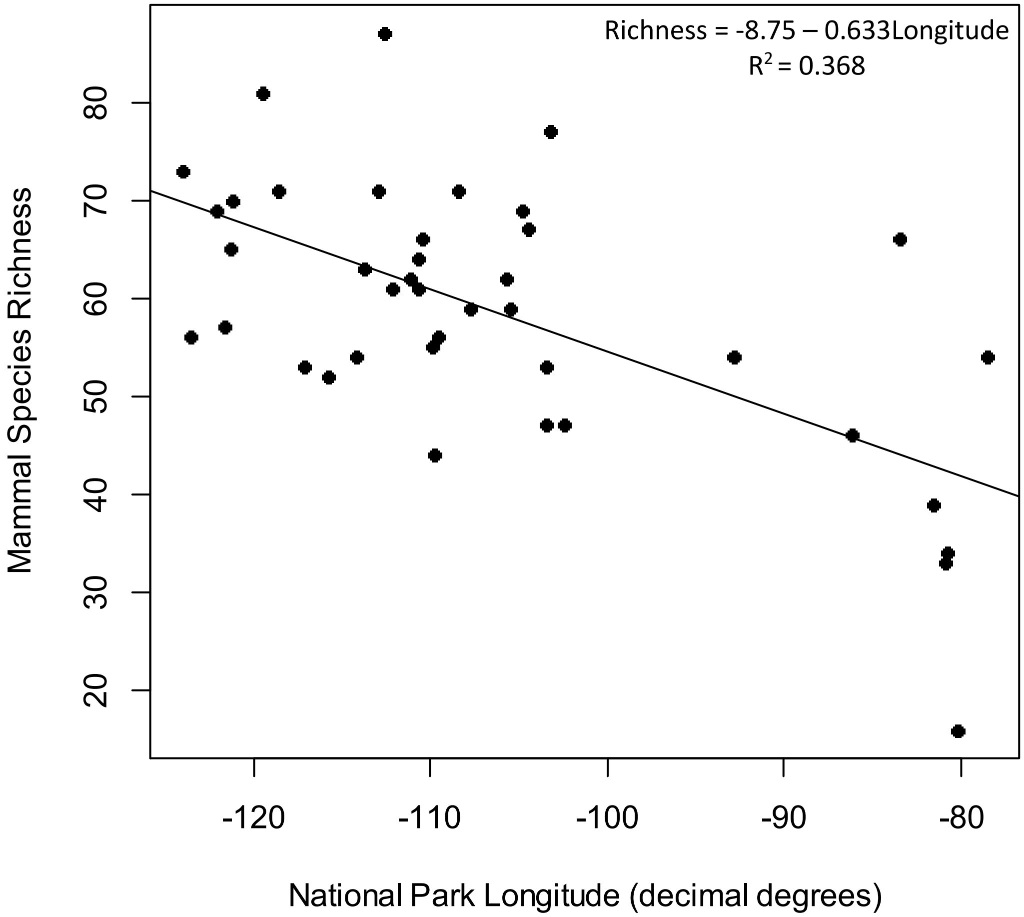

Figure 7. The relationship between mammal species richness and longitude (decimal degrees) in 40 national parks of the contiguous United States (R^2=0.368, F=23.7, df=1,38, $p<0.001$).

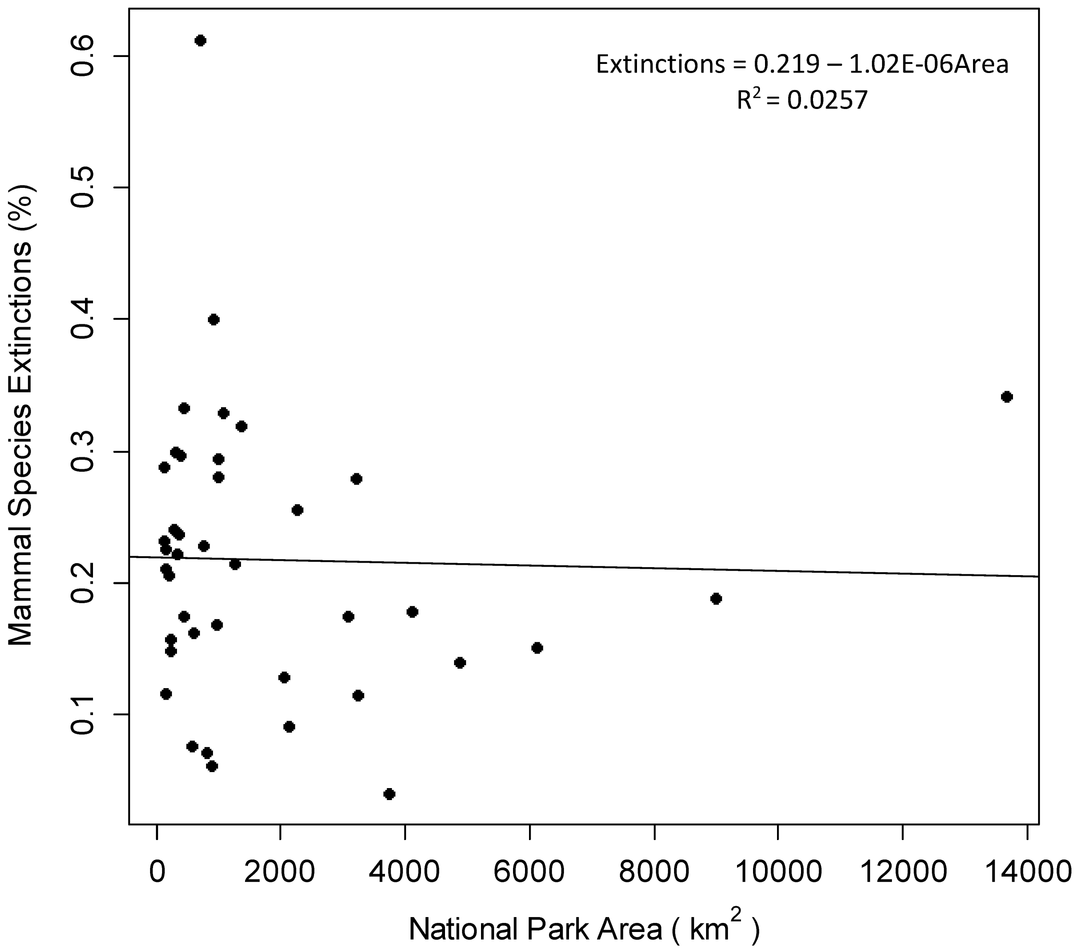

Figure 8. The relationship between the mammal species extinction percentage and area (km^2) in 40 national parks of the contiguous United States (R^2=0.0257, F=0.0248, df=1,38, p=0.876).

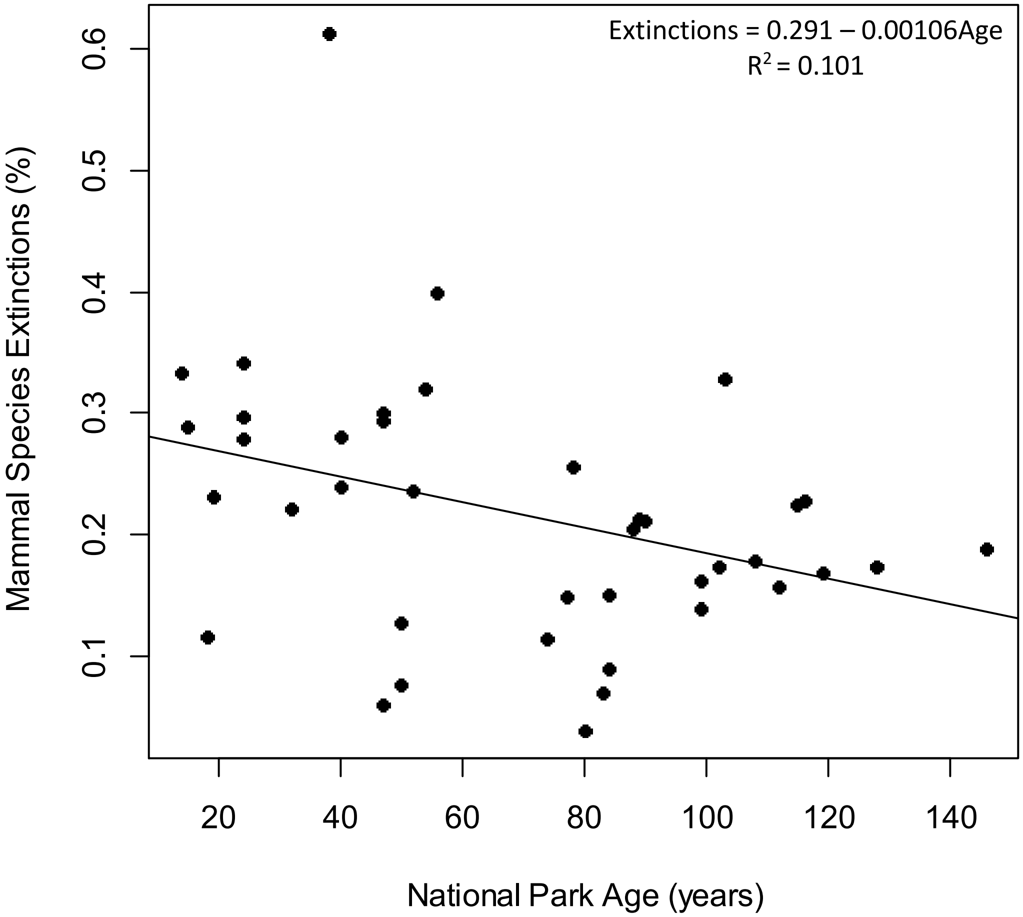

Figure 9. The relationship between mammal species extinction percentage and age (years) in 40 national parks of the contiguous United States (R^2=0.101, F=5.38, df=1,38, p=0.026).

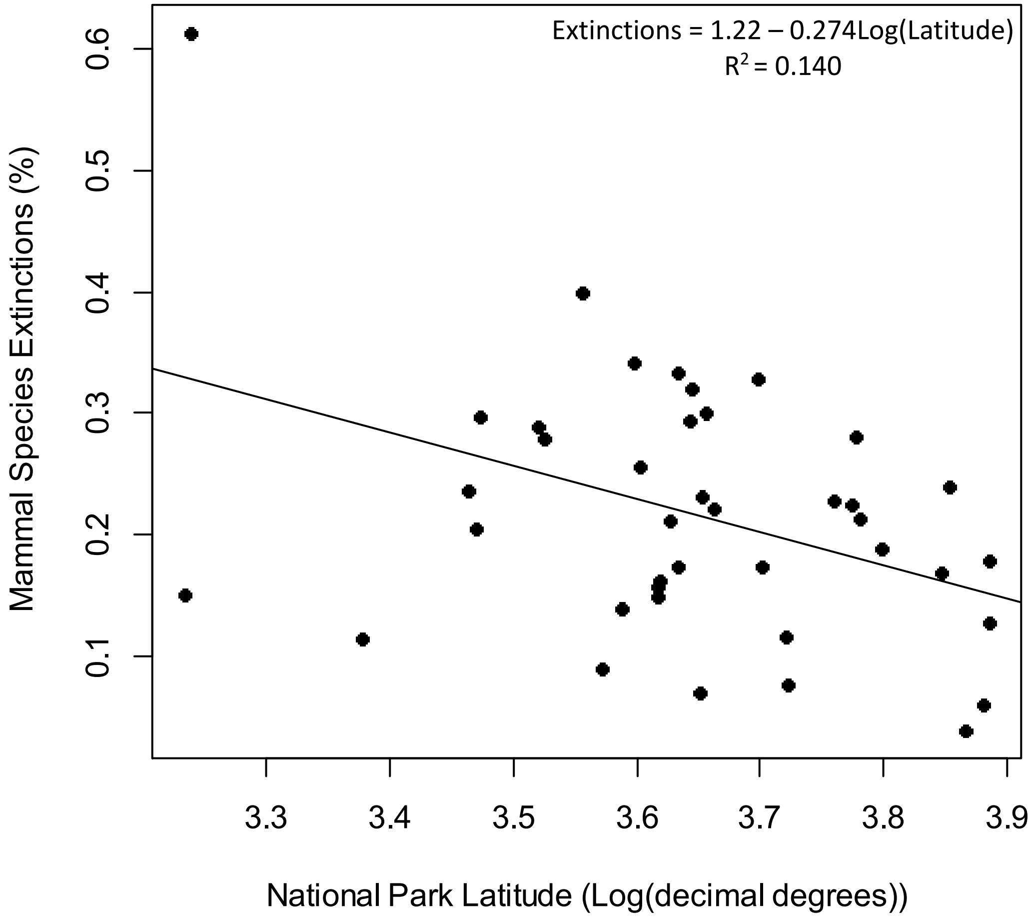

Figure 10. The relationship between mammal species extinction percentage and the log transform of latitude (decimal degrees) in 40 national parks of the contiguous United States (R^2=0.140, F=7.36, df=1,38, p=0.010).

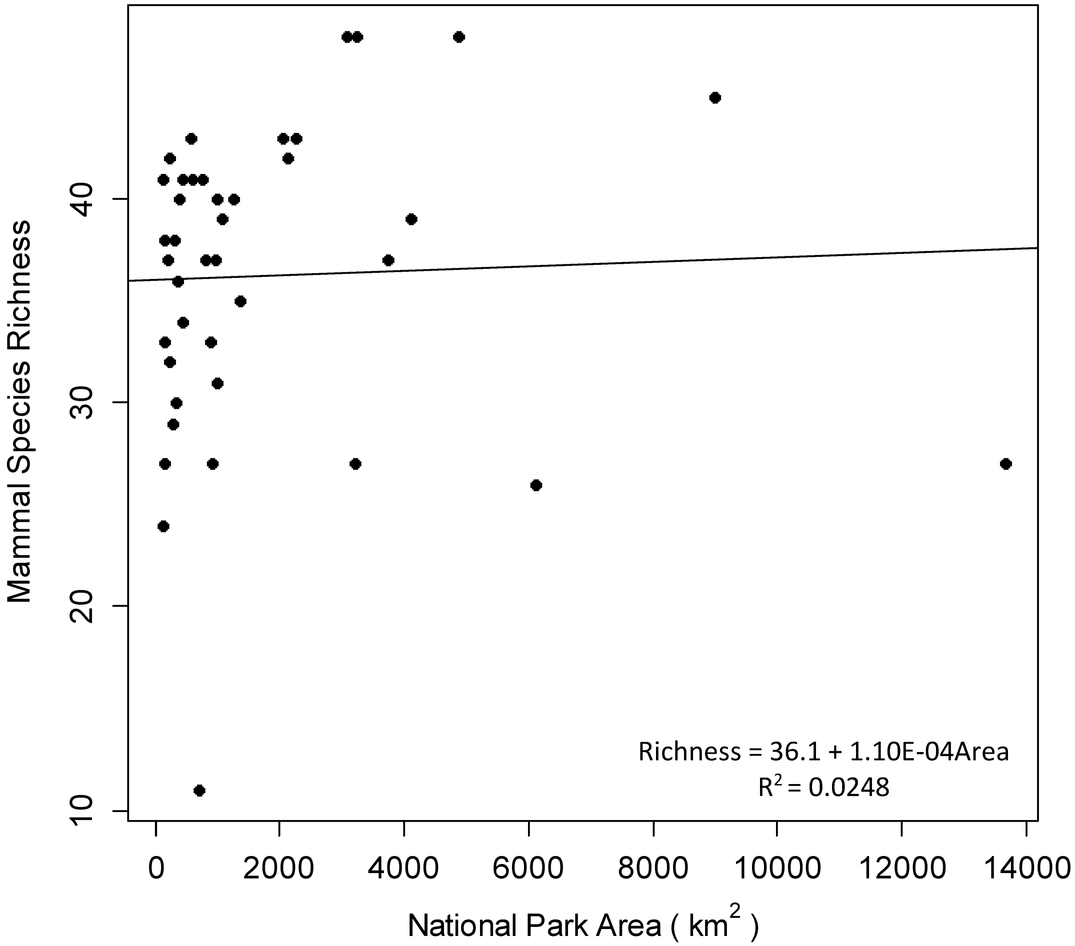

Figure 11. The relationship between mammal species richness (not including rodents) and area (km^2) in 40 national parks of the contiguous United States (R^2=0.0248, F=0.0576, df=1,38, p=0.812).

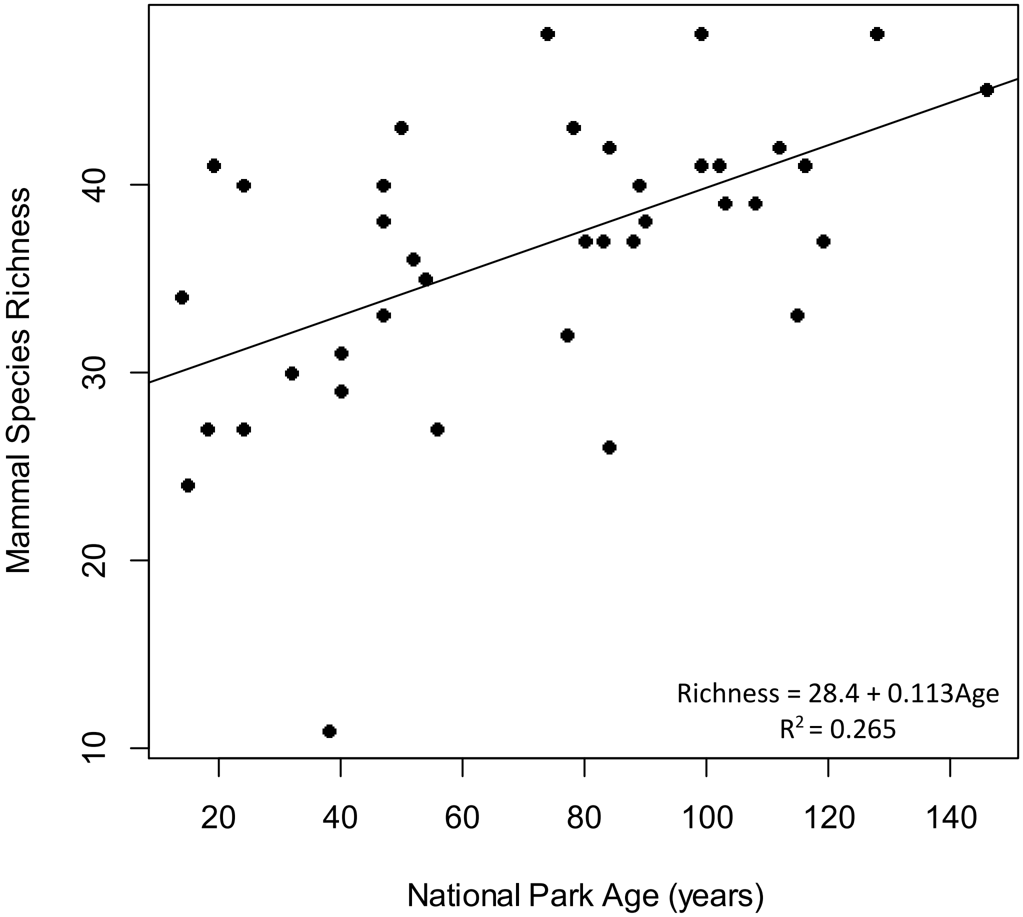

Figure 12. The relationship between mammal species richness (not including rodents) and age (years) in 40 national parks of the contiguous United States (R^2=0.265, F=15.1, df=1,38, $p<0.001$).

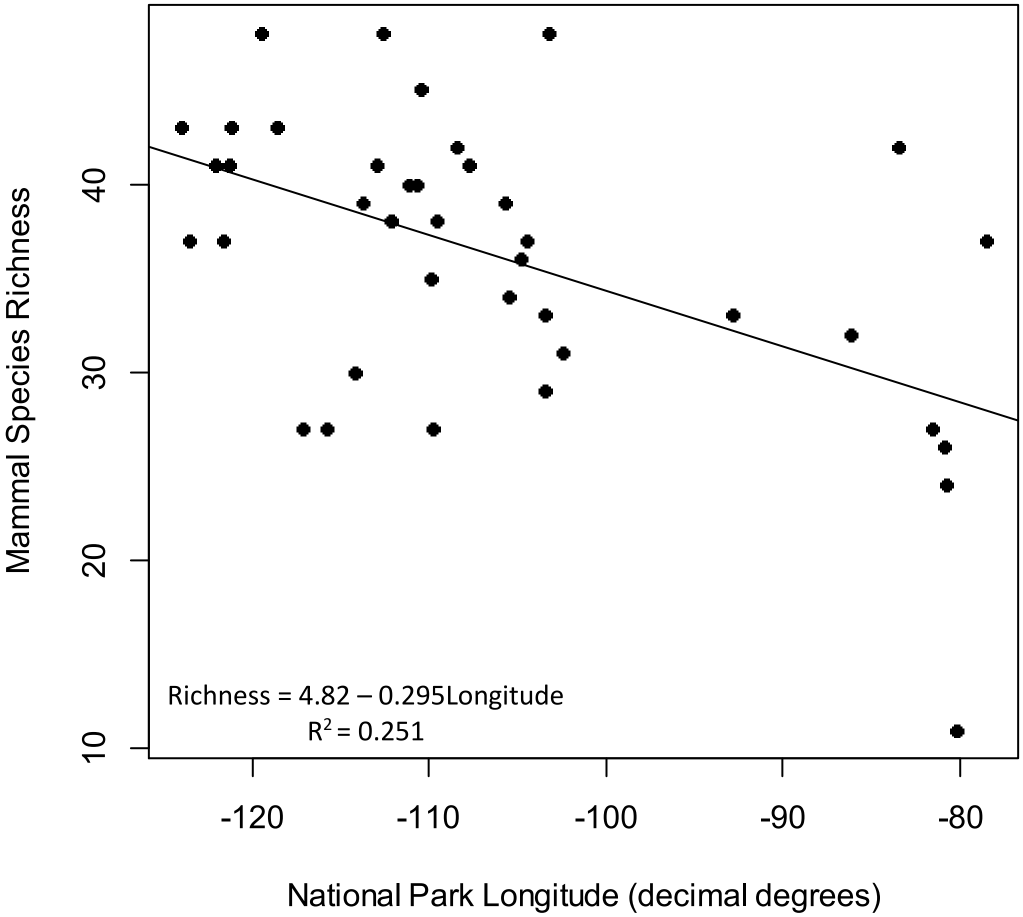

Figure 13. The relationship between mammal species richness (not including rodents) and longitude (decimal degrees) in 40 national parks of the contiguous United States ($R^2=0.251$, $F=14.08$, $df=1,38$, $p<0.001$).

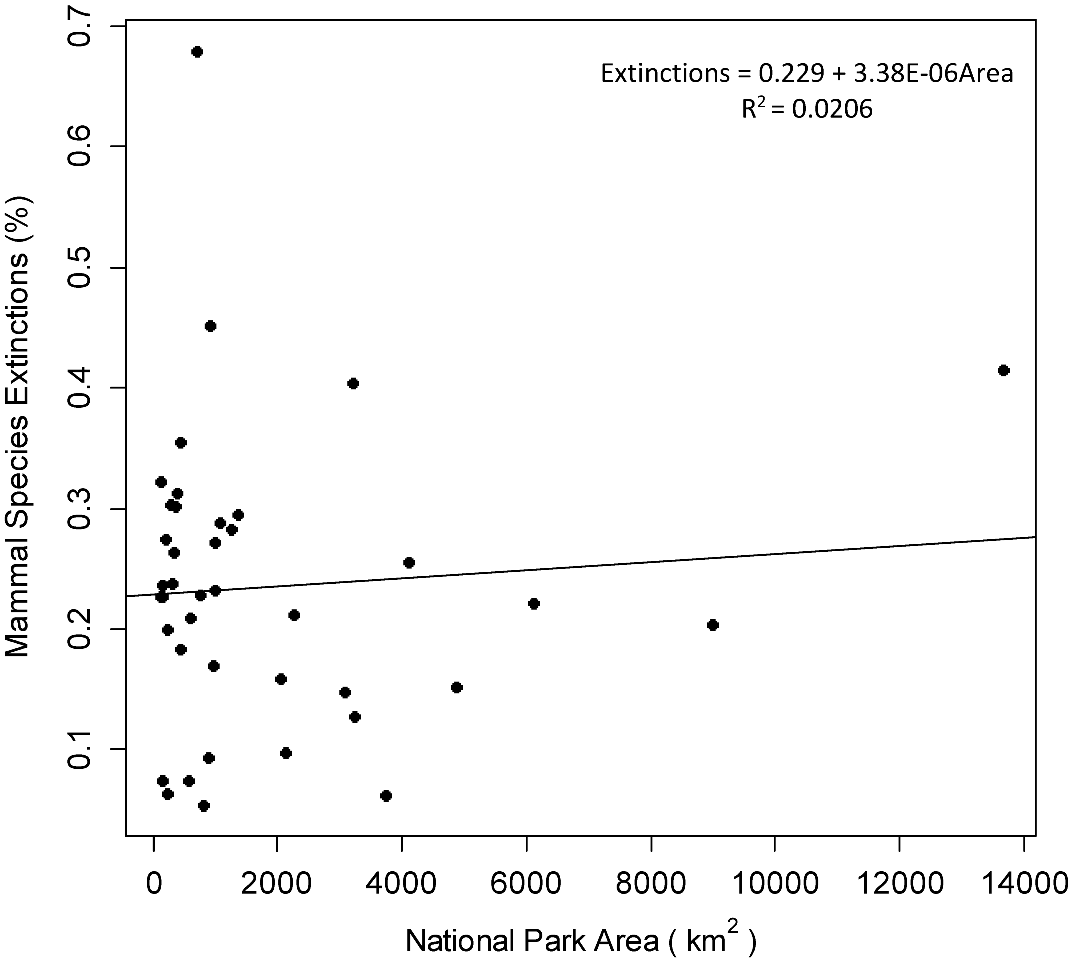

Figure 14. The relationship between mammal (not including rodents) species extinction percentage and area (km^2) in 40 national parks of the contiguous United States (R^2=0.0206, F=0.212, df=1,38, p=0.648).

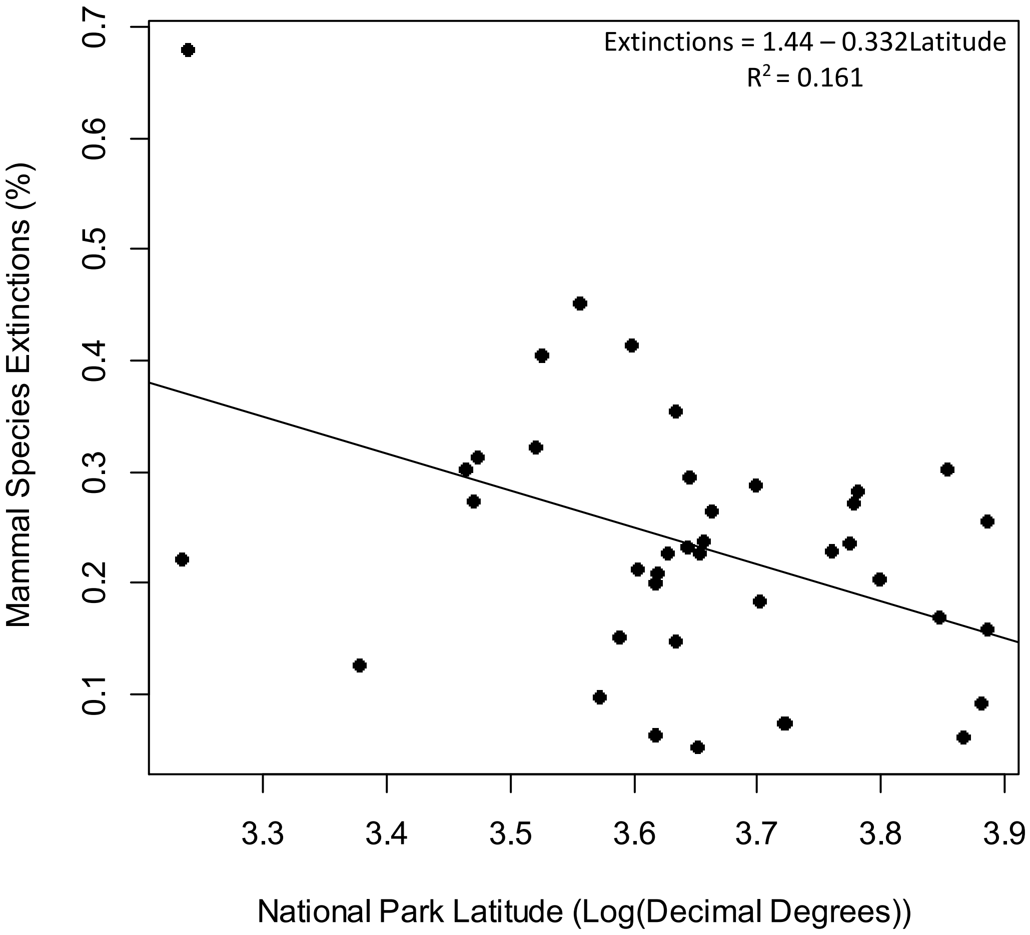

Figure 15. The relationship between mammal (not including rodents) species extinction percentage and the log transform of latitude (decimal degrees) in 40 national parks of the contiguous United States (R^2=0.161, F=8.50, df=1,38, p=0.006).

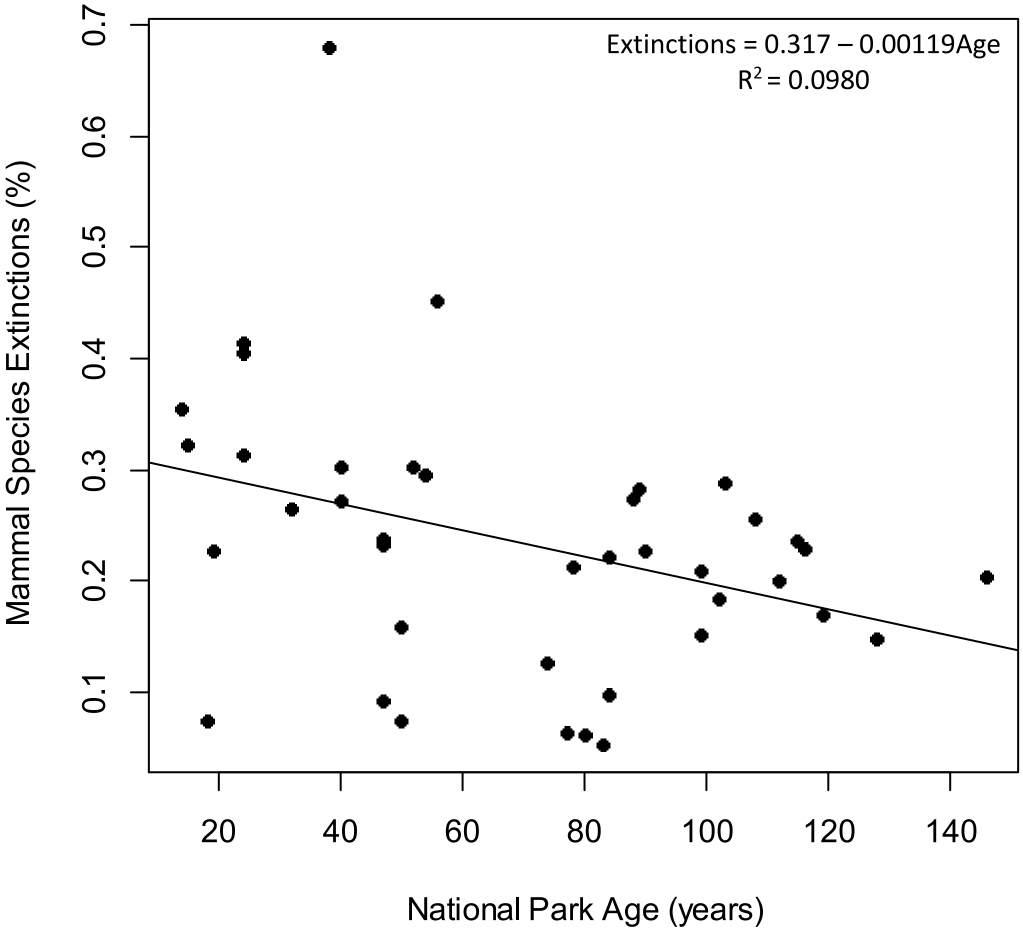

Figure 16. The relationship between mammal (not including rodents) species extinctions percentage and age (years) in 40 national parks of the contiguous United States (R^2=0.098, F=5.24, df=1,38, p=0.028).

APPENDIX A

Untransformed values for predictor variables used in the models of this study.

National Park	Age	Longitude	Latitude	Area
Arches National Park	47	-109.58635	38.72254	310.3
Badlands National Park	40	-102.48326	43.68544	982.4
Big Bend National Park	74	-103.22943	29.29738	3242.2
Biscayne National Park	38	-80.21025	25.49049	700
Black Canyon of the Gunnison National Park	19	-107.72442	38.57801	124.6
Bryce Canyon National Park	90	-112.18271	37.58390	145
Canyonlands National Park	54	-109.88011	38.24514	1366.2
Capitol Reef National Park	47	-111.17640	38.17732	979
Carlsbad Caverns National Park	88	-104.55299	32.14087	189.3
Congaree National Park	15	-80.74867	33.79187	107.4
Crater Lake National Park	116	-122.13275	42.94106	741.5
Cuyahoga Valley National Park	18	-81.57101	41.25918	131.8
Death Valley National Park	24	-117.13262	36.48393	13650.3
Everglades National Park	84	-80.88182	25.37217	6106.4
Glacier National Park	108	-113.80032	48.68330	4100
Great Basin National Park	32	-114.25797	38.94610	321.3
Grand Canyon National Park	99	-112.68425	36.17224	4862.9
Great Sand Dunes National Park & Preserve	14	-105.49672	37.83361	434.4
Great Smoky Mountains National Park	84	-83.50853	35.60057	2114.2
Grand Teton National Park	89	-110.70549	43.81816	1254.7
Guadalupe Mountains National Park	52	-104.88554	31.92301	349.5
Joshua Tree National Park	24	-115.83975	33.91397	3199.6
Lassen Volcanic National Park	102	-121.40760	40.49350	431.4
Mammoth Cave National Park	77	-86.13089	37.19758	218.6
Mesa Verde National Park	112	-108.46241	37.23905	212.4
Mount Rainier National Park	119	-121.70563	46.86092	956.6
North Cascades National Park	50	-121.20543	48.71113	2042.8
Olympic National Park	80	-123.66611	47.80324	3733.8
Petrified Forest National Park	56	-109.78776	34.98371	895.9
Redwood National Park	50	-124.03166	41.37133	562.5
Rocky Mountain National Park	103	-105.69728	40.35546	1075.6
Saguaro National Park	24	-110.75736	32.20904	371.2
Sequoia and Kings Canyon National Park	78	-118.58738	36.71172	2240.4
Shenandoah National Park	83	-78.46910	38.49177	806.2
Theodore Roosevelt National Park	40	-103.42997	47.17570	285.1
Voyageurs National Park	47	-92.83810	48.48355	883
Wind Cave National Park	115	-103.43948	43.58009	137.5

Yellowstone National Park	146	-110.54720	44.59644	8983.2
Yosemite National Park	128	-119.55714	37.84832	3082.7
Zion National Park	99	-113.02644	37.29824	595.8

APPENDIX B

Values for response variables used in bird models.

National Park	Bird current richness	Bird historic richness	Bird extinctions	Bird percent extinctions
Arches National Park	177	198	50	0.253
Badlands National Park	204	212	41	0.194
Big Bend National Park	402	247	14	0.057
Biscayne National Park	223	241	59	0.245
Black Canyon of the Gunnison National Park	168	206	62	0.301
Bryce Canyon National Park	195	199	35	0.176
Canyonlands National Park	197	195	34	0.174
Capitol Reef National Park	231	200	31	0.155
Carlsbad Caverns National Park	360	231	16	0.069
Congaree National Park	186	211	43	0.204
Crater Lake National Park	172	221	68	0.308
Cuyahoga Valley National Park	233	220	19	0.086
Death Valley National Park	374	228	7	0.031
Everglades National Park	343	247	6	0.024
Glacier National Park	237	215	32	0.149
Great Basin National Park	164	185	54	0.292
Grand Canyon National Park	353	236	3	0.013
Great Sand Dunes National Park & Preserve	226	215	31	0.144
Great Smoky Mountains National Park	219	212	22	0.104
Grand Teton National Park	192	203	34	0.166
Guadalupe Mountains National Park	262	236	55	0.233
Joshua Tree National Park	245	239	48	0.201
Lassen Volcanic National Park	199	204	40	0.196
Mammoth Cave National Park	163	217	65	0.300
Mesa Verde National Park	203	211	48	0.228
Mount Rainier National Park	152	200	70	0.350
North Cascades National Park	215	222	42	0.189
Olympic National Park	253	220	20	0.091
Petrified Forest National Park	219	200	40	0.200
Redwood National Park	302	243	16	0.066
Rocky Mountain National Park	246	212	30	0.142
Saguaro National Park	206	264	86	0.326
Sequoia and Kings Canyon National Park	205	224	64	0.286
Shenandoah National Park	190	216	39	0.181
Theodore Roosevelt National Park	155	207	74	0.358

Voyageurs National Park	228	199	9	0.045
Wind Cave National Park	210	203	38	0.187
Yellowstone National Park	278	209	10	0.048
Yosemite National Park	261	220	24	0.109
Zion National Park	252	206	15	0.073

APPENDIX C

Values for response variables used in mammal models.

National Park	Mammal current richness	Mammal historic richness	Mammal extinctions	Mammal percent extinctions
Arches National Park	56	70	21	0.300
Badlands National Park	47	57	16	0.281
Big Bend National Park	77	78	9	0.115
Biscayne National Park	16	31	19	0.613
Black Canyon of the Gunnison National Park	59	69	16	0.232
Bryce Canyon National Park	61	71	15	0.211
Canyonlands National Park	55	75	24	0.320
Capitol Reef National Park	62	78	23	0.295
Carlsbad Caverns National Park	67	73	15	0.206
Congaree National Park	34	45	13	0.289
Crater Lake National Park	69	83	19	0.229
Cuyahoga Valley National Park	39	43	5	0.116
Death Valley National Park	53	76	26	0.342
Everglades National Park	33	33	5	0.152
Glacier National Park	63	67	12	0.179
Great Basin National Park	54	63	14	0.222
Grand Canyon National Park	87	86	12	0.140
Great Sand Dunes National Park & Preserve	59	78	26	0.333
Great Smoky Mountains National Park	66	66	6	0.091
Grand Teton National Park	61	70	15	0.214
Guadalupe Mountains National Park	69	76	18	0.237
Joshua Tree National Park	52	68	19	0.279
Lassen Volcanic National Park	65	63	11	0.175
Mammoth Cave National Park	46	47	7	0.149
Mesa Verde National Park	71	76	12	0.158
Mount Rainier National Park	57	65	11	0.169
North Cascades National Park	70	70	9	0.129
Olympic National Park	56	50	2	0.040
Petrified Forest National Park	44	65	26	0.400
Redwood National Park	73	65	5	0.077
Rocky Mountain National Park	62	82	27	0.329
Saguaro National Park	64	84	25	0.298
Sequoia and Kings Canyon National Park	71	86	22	0.256
Shenandoah National Park	54	56	4	0.071
Theodore Roosevelt National Park	47	54	13	0.241

Voyageurs National Park	54	49	3	0.061
Wind Cave National Park	53	62	14	0.226
Yellowstone National Park	66	74	14	0.189
Yosemite National Park	81	86	15	0.174
Zion National Park	71	74	12	0.162

APPENDIX D

Values for response variables used in mammal models not including rodents.

National Park	Mammal current richness	Mammal historic richness	Mammal extinctions	Mammal percent extinctions
Arches National Park	11	25	17	0.680
Badlands National Park	24	31	10	0.323
Big Bend National Park	26	27	6	0.222
Biscayne National Park	27	27	2	0.074
Black Canyon of the Gunnison National Park	27	41	17	0.415
Bryce Canyon National Park	27	42	17	0.405
Canyonlands National Park	27	42	19	0.452
Capitol Reef National Park	29	33	10	0.303
Carlsbad Caverns National Park	30	34	9	0.265
Congaree National Park	31	33	9	0.273
Crater Lake National Park	32	31	2	0.065
Cuyahoga Valley National Park	33	32	3	0.094
Death Valley National Park	33	38	9	0.237
Everglades National Park	34	45	16	0.356
Glacier National Park	35	44	13	0.296
Great Basin National Park	36	43	13	0.302
Grand Canyon National Park	37	40	11	0.275
Great Sand Dunes National Park & Preserve	37	41	7	0.171
Great Smoky Mountains National Park	37	32	2	0.063
Grand Teton National Park	37	37	2	0.054
Guadalupe Mountains National Park	38	42	10	0.238
Joshua Tree National Park	38	44	10	0.227
Lassen Volcanic National Park	39	43	11	0.256
Mammoth Cave National Park	39	45	13	0.289
Mesa Verde National Park	40	43	10	0.233
Mount Rainier National Park	40	46	13	0.283
North Cascades National Park	40	51	16	0.314
Olympic National Park	41	44	10	0.227
Petrified Forest National Park	41	48	11	0.229
Redwood National Park	41	38	7	0.184
Rocky Mountain National Park	41	43	9	0.209
Saguaro National Park	42	41	4	0.098
Sequoia and Kings Canyon National Park	42	45	9	0.200
Shenandoah National Park	43	44	7	0.159
Theodore Roosevelt National Park	43	40	3	0.075

Voyageurs National Park	43	47	10	0.213
Wind Cave National Park	45	49	10	0.204
Yellowstone National Park	48	47	6	0.128
Yosemite National Park	48	46	7	0.152
Zion National Park	48	47	7	0.149

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